North American Journal of Fisheries Management 23:362–375, 2003
American Fisheries Society 2003

Influence of Flow and Temperature on Survival of Wild Subyearling Fall Chinook Salmon in the Snake River

WILLIAM P. CONNOR* AND HOWARD L. BURGE

U.S. Fish and Wildlife Service,
Post Office Box 18,
Ahsahka, Idaho 83520, USA

JOHN R. YEARSLEY

U.S. Environmental Protection Agency,
1200 Sixth Avenue,
Seattle, Washington 98101-9797, USA

THEODORE C. BJORNN[1]

U.S. Geological Survey,
Idaho Cooperative Fish and Wildlife Research Unit,
University of Idaho,
Moscow, Idaho 83843, USA

Abstract.—Summer flow augmentation to increase the survival of wild subyearling fall chinook salmon *Oncorhynchus tshawytscha* is implemented annually to mitigate for the development of the hydropower system in the Snake River basin, but the efficacy of this practice has been disputed. We studied some of the factors affecting survival of wild subyearling fall chinook salmon from capture, tagging, and release in the free-flowing Snake River to the tailrace of the first dam encountered by smolts en route to the sea. We then assessed the effects of summer flow augmentation on survival to the tailrace of this dam. We tagged and released 5,030 wild juvenile fall chinook salmon in the free-flowing Snake River from 1998 to 2000. We separated these tagged fish into four sequential within-year release groups termed cohorts ($N = 12$). Survival probability estimates (mean ± SE) to the tailrace of the dam for the 12 cohorts when summer flow augmentation was implemented ranged from 36% ± 4% to 88% ± 5%. We fit an ordinary least-squares multiple regression model from indices of flow and temperature that explained 92% ($N = 12$; $P < 0.0001$) of the observed variability in cohort survival. Survival generally increased with increasing flow and decreased with increasing temperature. We used the regression model to predict cohort survival for flow and temperature conditions observed when summer flow augmentation was implemented and for approximated flow and temperature conditions had the summer flow augmentation not been implemented. Survival of all cohorts was predicted to be higher when flow was augmented than when flow was not augmented because summer flow augmentation increased the flow levels and decreased the temperatures fish were exposed to as they moved seaward. We conclude that summer flow augmentation increases the survival of young fall chinook salmon.

Survival of chinook salmon *Oncorhynchus tshawytscha* smolts during seaward migration is affected by biotic factors, some of which are controlled by the physical environment. Researchers have proposed that streamflow and temperature act together to influence survival of chinook salmon smolts (Kjelson et al. 1982; Kjelson and Brandes 1989; Connor et al. 1998). Dams have altered the flow and water temperature regimes of rivers in the western United States, thereby contributing to declines in abundance of many stocks of chinook salmon by reducing smolt survival (e.g., Raymond 1988; Yoshiyama et al. 1988).

Raymond (1979) was the first to estimate survival for yearling Snake River spring and summer chinook salmon smolts, and to relate a decline in survival over years to dam construction. From 1966 to 1968, Raymond (1979) estimated that survival from the Salmon River to Ice Harbor Dam (Figure 1) for yearling spring and summer chinook salmon smolts was 85–95%. Between 1970 and 1975, Lower Monumental and Little Goose dams (Figure 1) were completed, and smolt survival estimates to Ice Harbor Dam decreased to 10–50% (Raymond 1979). Raymond (1979) concluded that during high flow years, lethal levels of dissolved gases killed yearling spring and summer chinook

* Corresponding author: william_connor@fws.gov
[1] Deceased

Received December 14, 2001; accepted July 22, 2002

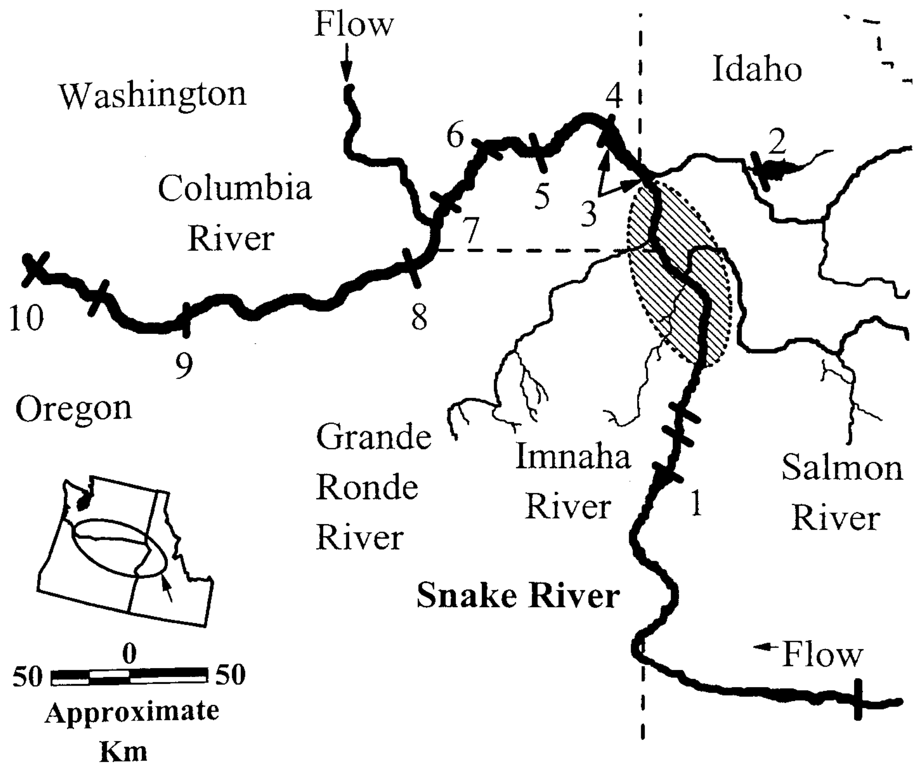

FIGURE 1.—Locations of the free-flowing Snake River where adult fall chinook salmon spawn and their offspring were captured by beach seine (cross-hatched ellipse; river kilometer [rkm] 224 to rkm 361), and other landmarks mentioned in the text. The locations are as follows: (1) Brownlee Reservoir and Brownlee (upstream most), Oxbow, and Hells Canyon dams; (2) Dworshak Dam and Reservoir; (3) Lower Granite Reservoir; (4) Lower Granite Dam (passive integrated transponder [PIT]-tag monitoring); (5) Little Goose Dam (PIT-tag monitoring); (6) Lower Monumental Dam (PIT-tag monitoring); (7) Ice Harbor Dam; (8) McNary Dam (PIT-tag monitoring); (9) John Day Dam (PIT-tag monitoring); and (10) Bonneville Dam (PIT-tag monitoring).

salmon smolts, whereas in low flow years, mortality resulted from low reservoir water velocities, delayed reservoir passage, predation, and passage via dam powerhouses.

Wild subyearling chinook salmon that pass downstream in the lower Snake River reservoirs from May to August include spring, summer, and fall-run juveniles that are listed under the Endangered Species Act (NMFS 1992). Wild fall chinook salmon typically compose the majority of the subyearling smolts that pass downstream during summer in the lower Snake River (Connor et al. 2001a). The minority is composed of wild spring and summer chinook salmon that disperse long distances from natal streams into the Snake River, where they adopt an ocean-type life history similar to that of fall chinook salmon (Connor et al. 2001a, 2001b). For simplicity, we refer to all of the wild subyearling chinook salmon that inhabit the shorelines of the Snake River as fall chinook salmon.

Dam construction changed juvenile fall chinook salmon life history in the Snake River basin by eliminating production in the relatively warmer water of the historical spawning area, thereby restricting spawning to less-productive, cooler reaches of river (Connor et al. 2002). This helps explain why present-day smolts migrate seaward during summer in contrast to their pre-dam counterparts that migrated seaward in late spring (Connor et al. 2002). Summer flow augmentation is intended to help recover the Snake River stock of fall chinook salmon by mitigating dam-caused changes in life history timing (NMFS 1995).

Summer flow augmentation is made up of releases of water from Dworshak Reservoir and reservoirs upstream of Brownlee Dam (NMFS 1995; Connor et al. 1998; Figure 1). These releases increase flow and decrease water temperature in Lower Granite Reservoir (Connor et al. 1998; Figure 1). Summer flow augmentation increases the rate of seaward movement of fall chinook salmon passing downstream in Lower Granite Reservoir, and reduces the time smolts take to pass Lower Granite Dam (Figure 1) by an average of 1–5 d (Connor et al. 2003).

Connor et al. (1998) concluded that summer flow augmentation also increased fall chinook salmon survival to Lower Granite Dam, and recommended that future studies should include sequential within-year releases of tagged fish and survival estimation based on a mark–recapture approach. In this paper, we estimate survival from release in the free-flowing Snake River to the tailrace of Lower Granite Dam with a mark–recapture approach. We test the effects of flow and water temperature on survival and then assess the effect of summer flow augmentation on survival.

Methods

Data collection.—We analyzed data collected on fall chinook salmon from 1998 to 2000. Data for these years were selected because sample sizes of tagged fall chinook salmon were large, and tagged fish were not handled as they passed Lower Granite Dam. Field personnel captured fall chinook salmon with a beach seine (Connor et al. 1998). Sampling typically started in April, soon after fry began emerging from the gravel, and was conducted 3 d/week at permanent stations. Once a majority of fish were at least 60 mm fork length, additional stations were sampled 1–2 d/week for three consecutive weeks. Sampling was discontinued in June or July, when the majority of fish had moved into Lower Granite Reservoir or points downstream.

Passive integrated transponder (PIT) tags (Prentice et al. 1990a) were inserted into parr that were 60 mm in fork length and longer (Connor et al. 1998). Tagged parr were released at the collection site after a 15-min recovery period. Some of the PIT-tagged fish were detected as smolts as they passed downstream in the juvenile bypass system of Lower Granite Dam (Matthews et al. 1977), which is equipped with PIT tag monitors (Prentice et al. 1990b).

After detection at Lower Granite Dam, the PIT-tagged smolts were routed through flumes back to the river. Smolts then had to pass seven more dams (Figure 1) to reach the Pacific Ocean. Little Goose, Lower Monumental, McNary, John Day, and Bonneville dams (Figure 1) were also equipped with monitoring systems that recorded the passage of PIT-tagged smolts in the bypass systems and then routed the bypassed fish back to the river.

Cohort survival.—The first step in the analysis was to divide the annual samples of PIT-tagged fall chinook salmon into four sequential within-year release groups referred to as cohorts. We divided the annual samples into cohorts based on estimated fry emergence dates. We estimated fry emergence date for each fish in two steps. First, the number of days since each PIT-tagged fish emerged from the gravel was calculated by subtracting 36 mm from its fork length measured at initial capture, and then dividing by the daily growth rate observed for recaptured PIT-tagged fish (range 0.9–1.3 mm/d; Connor and Burge, this issue). The 36-mm fork length for newly emergent fry was the mean of the observed minimum fork lengths. Second, emergence date was estimated for each fish by subtracting the estimated number of days since emergence from its date of initial capture, tagging, and release. We sorted the data in ascending order by estimated fry emergence date, and then divided it into four cohorts of approximately equal numbers of fish.

The single release–recapture model (Cormack 1964; Skalski et al. 1998) was used to estimate survival probability ($\pm$SE) to the tailrace of Lower Granite Dam for each cohort. We insured that the single release–recapture model fit the data by use of three assumption tests described by Burnham et al. (1987) and Skalski et al. (1998).

Variables.—Cohort survival was the dependent variable for the analysis. The predictor variables were: (1) tagging date, or the median day of year (day 1 = 1 January) fish from each cohort were captured, tagged, and released; (2) mean fork length (mm) at capture, tagging, and release for the fish of each cohort; (3) flow exposure index, calculated as the mean flow (m^3/s) measured at Lower Granite Dam by U.S. Army Corps of Engineers personnel during the period when the majority of smolts from each cohort passed the dam; and (4) water temperature exposure index, calculated as the mean temperature (°C) measured in the tailrace of Lower Granite Dam by U.S. Army Corps of Engineers personnel during the period when the majority of smolts from each cohort passed the dam.

To determine when the majority of smolts passed Lower Granite Dam, the PIT tag detection data were used to calculate a passage date distribution for each cohort including the 25th percentile, median, 75th percentile, range of non-outliers, and mild outliers (Figure 2). The date cutoffs for mild outliers were calculated as the 25th percentile minus the interquartile range multiplied by 1.5

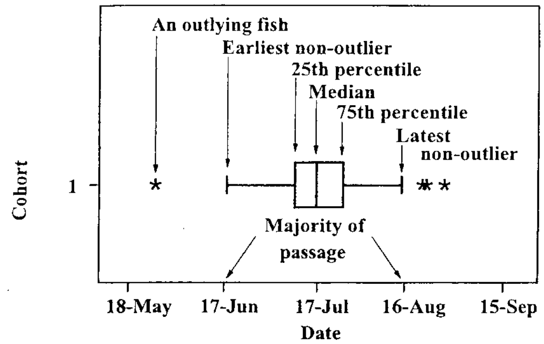

FIGURE 2.—An example of a passage date distribution for PIT-tagged wild subyearling fall chinook salmon at Lower Granite Dam, including the time period that was used to represent the majority of passage for calculating flow and water temperature exposure indices. The left whisker on the box plot extends back to the earliest detection date (17 June) that was later than or equal to the lower fence (25th percentile minus the interquartile range, multiplied by 1.5), and the right whisker extends forward to the detection date (16 August) that was earlier than or equal to the upper fence (75th percentile plus the interquartile range, multiplied by 1.5). The asterisks signify mild outliers (one asterisk represents one fish) that were earlier than the lower fence or later than the upper fence.

(i.e., the lower fence; Ott 1993), and the 75th percentile plus the interquartile range multiplied by 1.5 (i.e., the upper fence; Ott 1993). The left whisker on the box plot in Figure 2 extends back to the earliest detection date (17 June) that was later than or equal to the lower fence, and the right whisker extends forward to the detection date (16 August) that was earlier than or equal to the upper fence. The asterisks in Figure 2 signify mild outliers that were earlier than the lower fence or later than the upper fence (Ott 1993). All but the mild outliers were considered to be in the majority. The mean flow exposure index calculated based on the passage date distribution in Figure 2 would be the average of the mean daily flows measured in the tailrace of Lower Granite Dam between 17 June and 16 August.

Model selection.—We calculated Pearson's product-moment correlation coefficient (r) to test for colinearity among the predictor variables. Predictor variables that were correlated ($r \geq 0.6$; $P \leq 0.05$) were not entered into the same model.

We fit multiple regression models from every combination of non-collinear predictor variables. We compared fit among models based on Mallow's C_p scores (Dielman 1996), Akaike's information criteria (AIC; Akaike 1973), and the coefficient of determination (R^2). The final (i.e., best) regression model had a Mallow's Cp score similar to the number of parameters, the lowest AIC value, the high-

TABLE 1.—Median emergence dates, predictor variables, and estimates of survival probability (%; ±SE in parentheses) to the tailrace of Lower Granite Dam for each cohort of wild subyearling fall chinook salmon, 1998–2000. Predictor variables include: tagging date, defined as the median day of year of tagging; mean fork length (FL; mm) at tagging; flow (m^3/s), a flow exposure index calculated as the mean flow measured at Lower Granite Dam during the period when the majority of smolts passed the dam; and temperature (°C), a water temperature exposure index calculated as the mean temperature measured in the tailrace of Lower Granite Dam during the period when the majority of smolts passed the dam.

Cohort	N	Emergence date	Tagging date	FL	Flow	Temperature	Survival
1998							
1	515	7 Apr	140	80	2,344	17.6	70.8 (2.9)
2	515	15 Apr	141	75	2,021	18.7	66.1 (3.3)
3	515	23 Apr	153	73	1,898	19.0	52.8 (3.1)
4	515	7 May	167	70	1,299	19.8	35.6 (2.9)
1999							
1	441	20 Apr	147	80	2,378	16.3	87.7 (4.6)
2	440	30 Apr	153[a]	77	1,963	17.1	77.0 (3.8)
3	440	5 May	152[a]	70	2,116	16.7	81.2 (5.8)
4	440	13 May	167	68	1,353	18.3	36.4 (3.5)
2000							
1	303	6 Apr	130	77	1,510	16.7	57.1 (4.1)
2	302	15 Apr	144	77	1,296	17.6	53.4 (4.2)
3	302	22 Apr	146	77	1,274	17.8	44.4 (3.6)
4	302	29 Apr	158	71	859	18.5	35.7 (4.3)

[a] Fish from cohort 2 emerged earlier than the fish of cohort 3, but they were initially captured, tagged, and released later than cohort 3.

TABLE 2.—Mallow's C_p scores, Akaike's information criteria (AIC), and coefficients of determination (R^2) used to compare the fit of multiple regression models describing the survival of cohorts of wild subyearling fall chinook salmon from tagging in the Snake River to the tailrace of Lower Granite Dam, 1998–2000. Predictor variables are defined in Table 1.

C_p	AIC	R^2	Variables in model
2	44	0.92	Flow, temperature
4	46	0.92	FL, flow, temperature
4	46	0.92	Tagging date, flow, temperature

est R^2 value, and predictor variables with slope coefficients that differed significantly ($t \geq 2.0$; $P \leq 0.05$) from zero. Only the top three models are reported.

We made residual plots for each predictor variable in the final regression model, as described for flow in the following example. Estimated survival was regressed against temperature. The residuals from this regression were then plotted against flow. A line was then fit to the residuals by regressing them against flow. The resulting residual plots provided a better graphical representation of the relation between survival and flow because the variability in survival attributable to temperature had been removed.

Assessment of summer flow augmentation.—We assessed the effect of summer flow augmentation on cohort survival to the tailrace of Lower Granite Dam by comparing two predictions. First, we predicted cohort survival to the tailrace of Lower Granite Dam by entering the observed mean flow and water temperature exposure indices for each cohort into the final regression model. Cohort survival was then predicted a second time by entering mean flow and water temperature exposure indices, recalculated to remove effects of summer flow augmentation, into the final regression model.

The flow exposure index was recalculated after reducing Lower Granite Reservoir daily outflow by an approximation of the daily volume of water released for summer flow augmentation during 1 July–31 August from Dworshak Reservoir and reservoirs upstream of Brownlee Dam. The daily volume released from Dworshak Reservoir was calculated as the largest of two numbers: (1) the observed outflow at Dworshak Dam (Figure 1) minus observed inflow to Dworshak Reservoir, or (2) a minimum operational outflow of 28 m^3/s. For reservoirs upstream of Brownlee Dam, the daily volume was calculated in two steps: (1) 82 m^3/s (estimated flow released for augmentation from reservoirs upstream of Brownlee Reservoir) was sub-

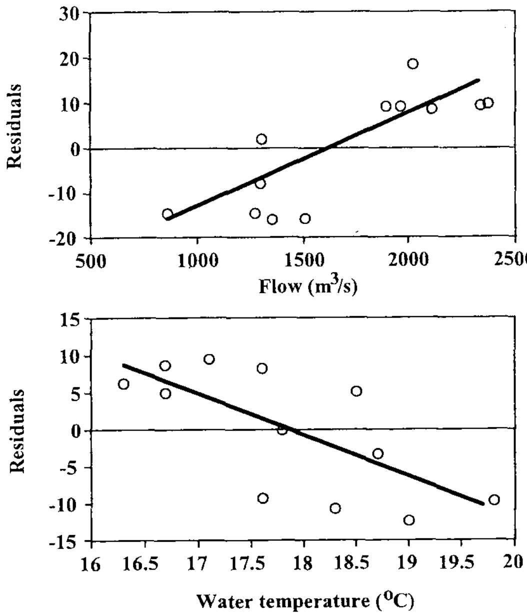

FIGURE 3.—Residual plots for flow (top) and temperature (bottom). Residuals are from ordinary least-squares multiple regression models fit to predict cohort survival from the predictor variables that are not on the x-axis. The line in each plot was predicted by regression of the residuals against the predictor variable on the x-axis.

tracted from daily inflow to Brownlee Reservoir, and (2) the resulting flow was subtracted from observed outflow at Hells Canyon Dam (Figure 1). Finally, the daily sum of the flow approximations for Dworshak Reservoir and reservoirs upstream of Brownlee Dam was subtracted from daily outflow observed at Lower Granite Dam. The Appendix gives the daily flow values for 1 July–31 August that were used to approximate the Lower Granite Reservoir flow that would have occurred if the summer flow augmentation had not been implemented.

The water temperature exposure index was recalculated with temperatures that were simulated for the tailrace of Lower Granite Dam under the approximated flow conditions that would have occurred without summer flow augmentation (Appendix). Water temperatures were simulated with a one-dimensional heat budget model developed for the Snake River by the U.S. Environmental Protection Agency (Yearsley et al. 2001). Past model validation showed that daily mean water temperatures simulated for July and August were within an average of 0.7°C of those observed (Yearsley et al. 2001).

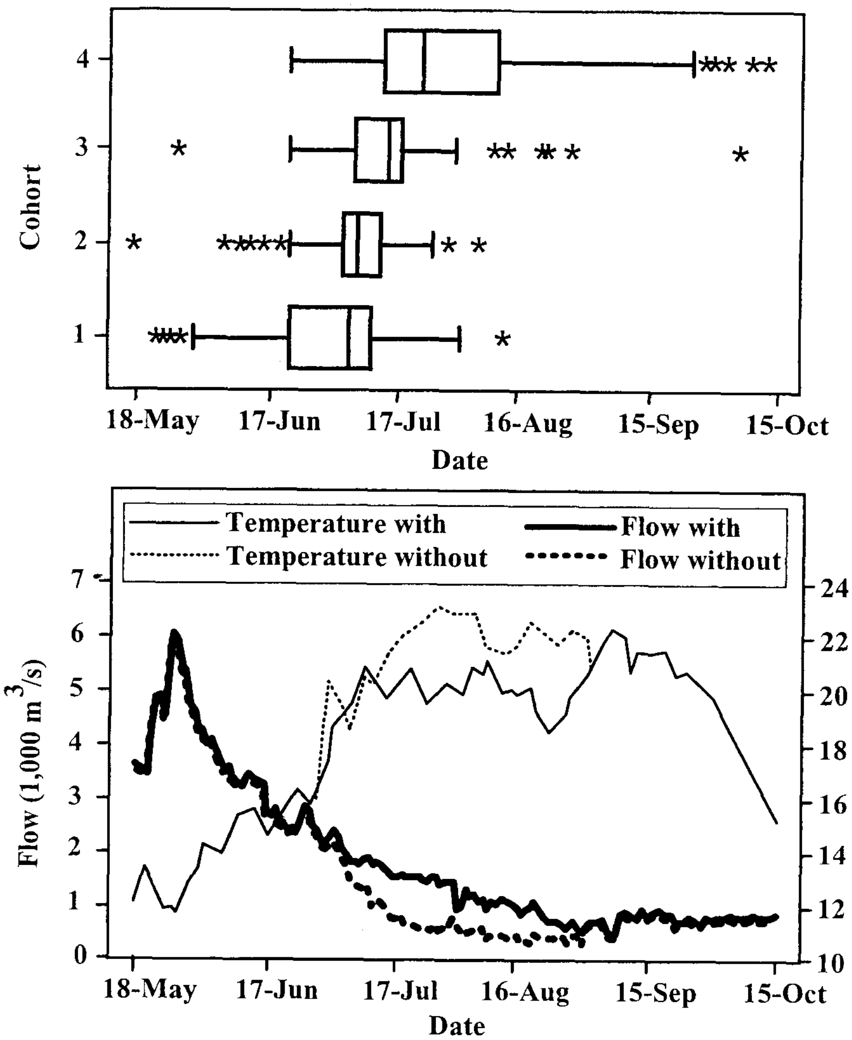

FIGURE 4.—Box plots showing passage timing at Lower Granite Dam for PIT-tagged wild subyearling fall chinook salmon from each of four cohorts in 1998 (top), and a comparison of the mean daily flows and water temperatures in Lower Granite Reservoir with (observed) and without (estimated) summer flow augmentation (bottom). See Figure 2 for a description of box plots.

Results

During the 3 years of the study, 5,030 fall chinook salmon were captured, PIT tagged, and released along the free-flowing Snake River. Annual sample sizes of PIT-tagged fall chinook salmon were 2,060 in 1998, 1,761 in 1999, and 1,209 in 2000. The number of fall chinook salmon in each of the resulting 12 cohorts was 302–515 (Table 1). Emergence dates, tagging dates, and water temperature exposure indices generally increased from cohort 1 to cohort 4 (Table 1). Flow exposure indices, fork lengths, and survival estimates generally decreased from cohort 1 to cohort 4 (Table 1).

Survival Modeling

Tagging date and fork length were negatively correlated ($N = 12$; $r = -0.76$; $P = 0.004$). Therefore, tagging date and fork length were not entered into the same multiple regression model. Fork length and flow ($N = 12$; $r = 0.47$; $P = 0.12$), fork length and temperature ($N = 12$; $r = -0.54$; $P = 0.07$), and flow and temperature ($N = 12$; $r = -0.45$; $P = 0.15$) were non-collinear.

The model that predicted cohort survival from flow and temperature had a Mallow's C_p score one less than the number of parameters, the lowest AIC value, and an R^2 of 0.92 (Table 2). The models

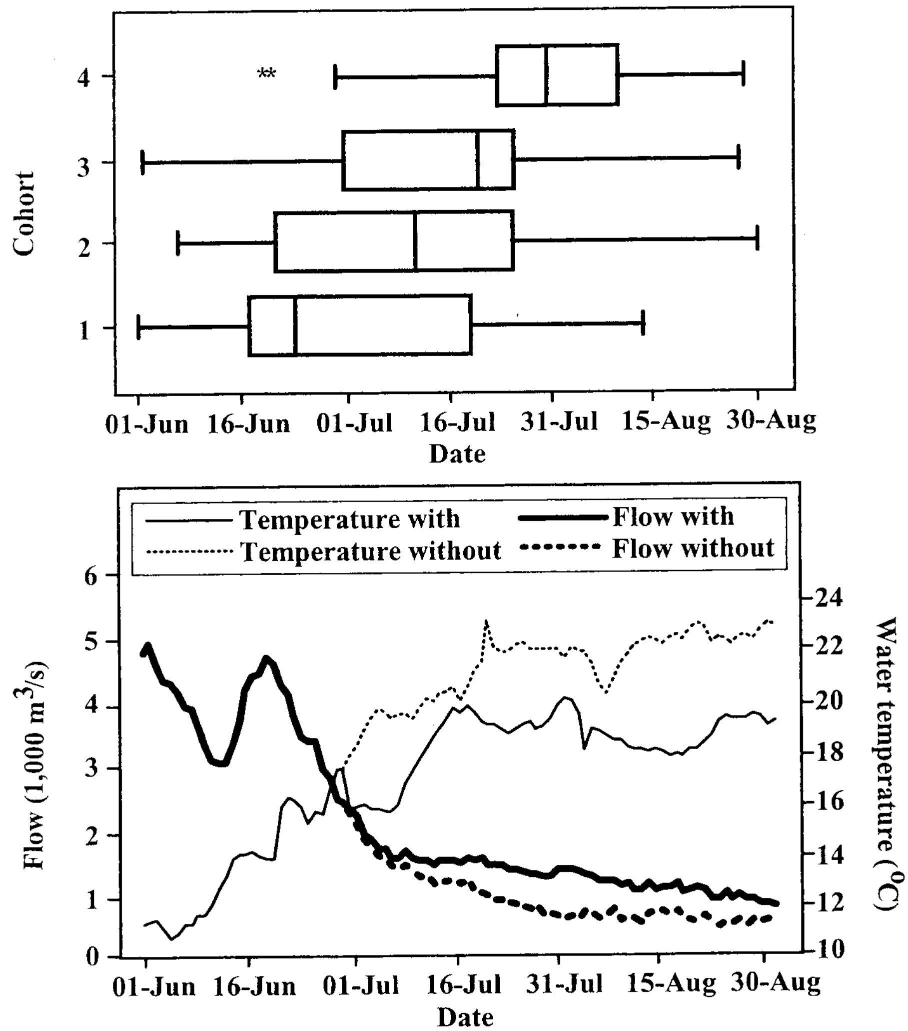

FIGURE 5.—Box plots showing passage timing at Lower Granite Dam for PIT-tagged wild subyearling fall chinook salmon from each of four cohorts in 1999 (top), and a comparison of the mean daily flows and water temperatures in Lower Granite Reservoir with (observed) and without (estimated) summer flow augmentation (bottom). See Figure 2 for a description of box plots.

that included fork length or tagging date had Mallow's C_p scores that equaled the number of parameters, relatively low AIC values, and R^2 values of 0.92 (Table 2), but the slope coefficients for fork length (t = 0.05; P = 0.96) and tagging date (t = 0.07; P = 0.94) did not differ significantly from zero.

The final multiple regression model was: cohort survival = 140.82753 + 0.02648(flow) − 7.14437(temperature). The final model was significant (N = 12; $P \leq 0.0001$), as were the slope coefficients for flow (t = 6.81; $P \leq 0.0001$) and temperature (t = −3.96; P = 0.003). Flow and temperature explained 92% of the observed variability in cohort survival to the tailrace of Lower Granite Dam. Cohort survival generally increased as flow increased, and decreased as temperature increased (Figure 3).

Assessment of Summer Flow Augmentation

Water releases for summer flow augmentation in 1998, 1999, and 2000 were generally timed to coincide with the passage of later migrating smolts at Lower Granite Dam (Figures 4–6). Therefore, later cohorts were usually predicted to accrue greater survival benefits than earlier cohorts (Table

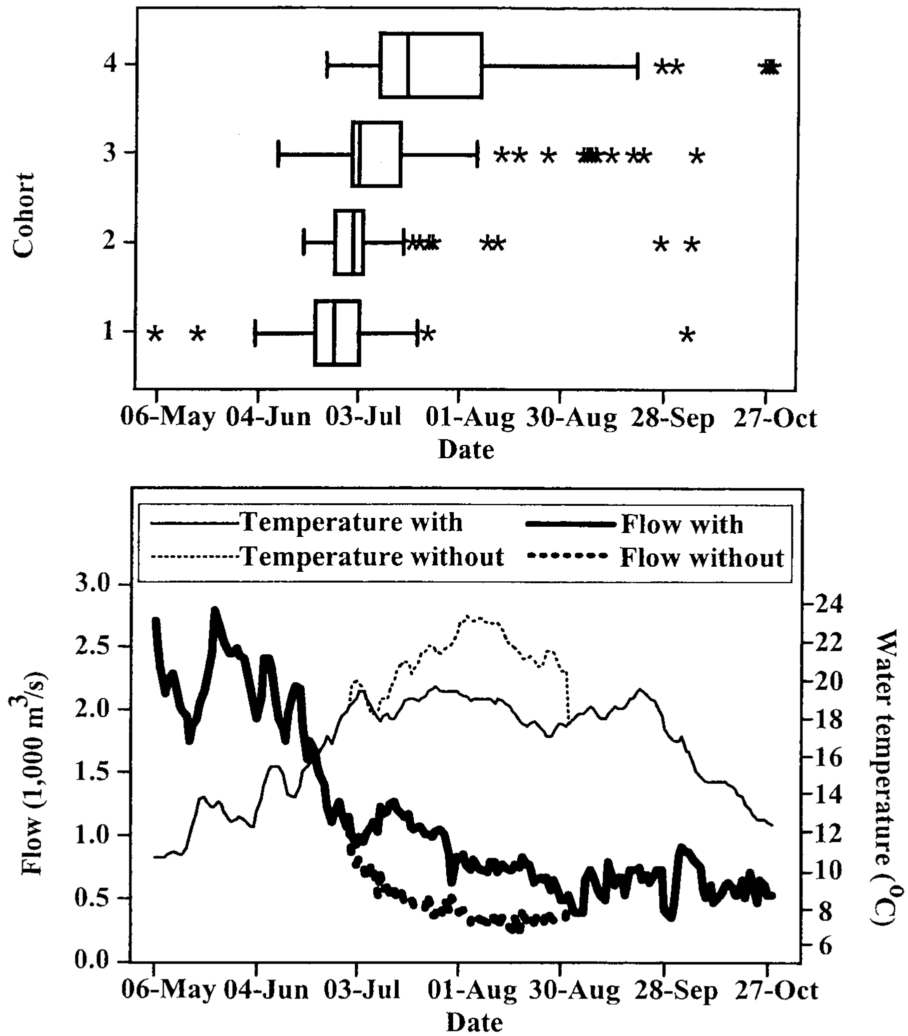

FIGURE 6.—Box plots showing passage timing at Lower Granite Dam for PIT-tagged wild subyearling fall chinook salmon from each of four cohorts in 2000 (top), and a comparison of the mean daily flows and water temperatures in Lower Granite Reservoir with (observed) and without (estimated) summer flow augmentation (bottom). See Figure 2 for a description of box plots.

3). For all cohorts, estimated survival to the tailrace of Lower Granite Dam was predicted to be higher when summer flow augmentation was implemented than when it was not implemented (Table 3; Figure 7).

Discussion

Survival of wild subyearling fall chinook salmon from release in the Snake River to the tailrace of Lower Granite Dam generally increased as flow increased, and decreased as temperature increased. Based on the regression model we developed, survival is predicted to change by approximately 3% with each change of 100 m^3/s in flow when temperature is held constant. The change in survival is approximately 7% for each 1°C increase or decrease in temperature when flow is held constant. Kjelson et al. (1982), Kjelson and Brandes (1989), and Connor et al. (1998) also reported that survival of subyearling chinook salmon during seaward migration is directly proportional to flow and inversely proportional to temperature.

Flow and temperature were closely correlated in the above three studies (e.g., $r = -0.999$; Connor et al. 1998), thus the researchers could not determine whether the high correlation between sur-

TABLE 3.—Predicted survival (%; ± 95% confidence interval in parentheses) to the tailrace of Lower Granite Dam for cohorts of wild subyearling fall chinook salmon tagged in the Snake River from 1995 to 1998. Predictions were made with the observed flow and water temperature indices in Table 1 (survival with), and with flow (m^3/s) and water temperature (°C) exposure indices recalculated to approximate conditions that would have occurred without flow augmentation (survival without).

Cohort	Survival with	Recalculated Flow	Recalculated Temperature	Survival without	Difference in survival
1998					
1	77.2 (6.5)	2,066	18.3	64.8 (5.8)	12.4
2	60.7 (6.6)	1,689	19.3	47.7 (7.0)	13.0
3	55.3 (6.8)	1,468	20.1	36.1 (9.3)	19.2
4	33.8 (8.0)	988	21.3	14.8 (13.1)	19.0
1999					
1	87.3 (7.5)	2,128	17.1	75.0 (5.2)	12.3
2	70.6 (4.7)	1,667	18.4	53.5 (4.3)	17.1
3	77.5 (5.8)	1,837	18.0	60.9 (4.0)	16.6
4	45.9 (4.6)	943	20.1	22.2 (9.4)	23.7
2000					
1	61.5 (6.7)	1,314	17.0	54.2 (6.8)	7.3
2	49.4 (5.5)	1,078	17.9	41.5 (6.5)	7.9
3	47.4 (5.3)	978	18.6	33.8 (6.7)	13.6
4	31.4 (7.5)	587	20.1	12.8 (10.6)	18.6

vival and one variable was caused by the other variable. Flows and temperatures were atypically uncorrelated ($r = -0.45$) from 1998 to 2000, therefore we were able to enter both of these predictor variables into the same multiple regression equation without biasing the regression coefficients. Both regression coefficients differed significantly from zero (flow $P \leq 0.0001$; temperature $P = 0.003$). We conclude that flow and temperature act together to influence fall chinook salmon survival.

Correlation does not imply causation unless the causal mechanisms can be identified with certainty. Flow and water temperature, however, are the two most plausible factors affecting survival, since fall chinook salmon are aquatic poikilotherms. We suggest that the two variables simultaneously assert their influence on survival. For example, flow influences rate of seaward movement (Berggren and Filardo 1993; Connor et al. 2003) and water turbidity at the same time temperature is regulating predation (Vigg and Burley 1991; Curet 1994; Anglea 1997). Fall chinook salmon that migrate downstream when flow is low and temperatures are warm might suffer high mortality because they are exposed for longer durations to actively feeding predators in clear water.

Slow downstream movement and late-summer passage associated with low flow levels (Connor et al. 2003) can also result in exposure to temperatures above 20°C. Prolonged exposure to temperatures above 20°C might disrupt fall chinook salmon growth, smoltification, and downstream movement, thereby exacerbating predation (Marine 1997). Temperatures above 20°C have also been associated with disease and stress-induced mortality (Connor, unpublished).

Management Implications

A discussion of the management implications of the results in this paper requires an understanding of the limitations on our study. Post-tagging mortality of cohorts released later in the summer would bias our analyses. Though Prentice et al. (1990a) found that delayed mortality of subyearling fall chinook salmon was low (range, 1–5%) 135–139 d after PIT tagging, their tests were not conducted at temperatures above 14.4°C. Research should be conducted on delayed mortality of PIT-tagged fall chinook salmon at temperatures above 14.4°C. We could not ascertain where PIT-tagged fall chinook salmon died en route to Lower Granite Dam. Our assessment of summer flow augmentation would be weakened if the majority of tagged fish died in the free-flowing Snake River before flow was augmented. We relied on simple approximations of the flow volumes released for summer flow augmentation to simulate temperatures in Lower Granite Reservoir, and to predict fall chinook salmon survival without summer flow augmentation. Advanced hydrological and temperature modeling and more accurate flow and temperature data will be required to accurately describe the flow and temperature effects of summer flow augmentation in Lower Granite Reservoir.

In spite of these limitations, we believe the results in this paper support summer flow augmentation as a beneficial interim recovery measure for Snake River fall chinook salmon. Survival for all cohorts was predicted to be higher with summer flow augmentation than without augmentation. We conclude that increases in flow and decreases in water temperature resulting from summer flow augmentation increase survival of young fall chinook salmon.

Although summer flow augmentation likely increased survival of fall chinook salmon passing downstream in Lower Granite Reservoir, mortality is probably still higher than before dams were constructed. When the lower Snake River was still free-flowing, the latest emigrating juvenile chinook salmon were exposed to mean June flows of approximately 2,800 m^3/s in 1954 and 3,800 m^3/s in

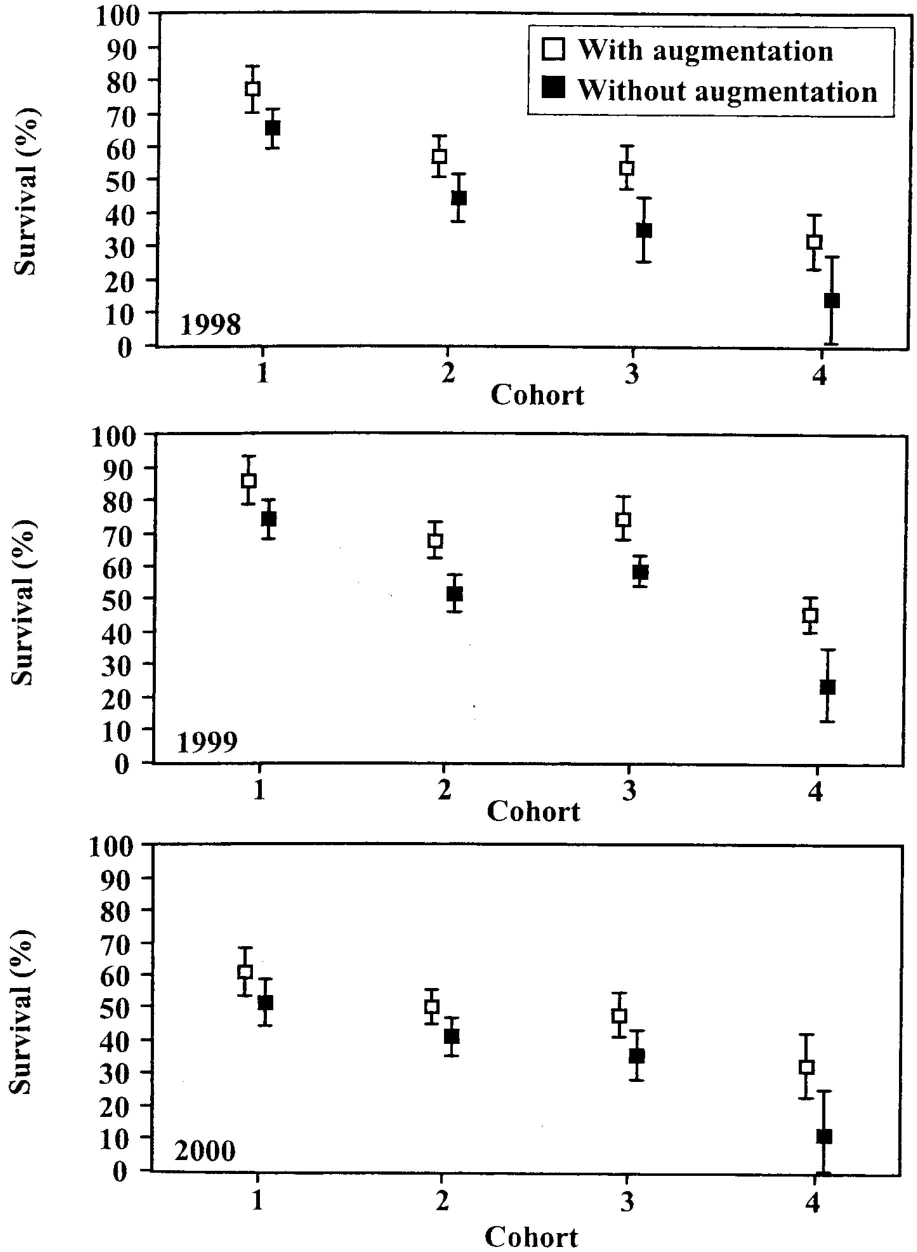

FIGURE 7.—Survival (±95% confidence interval) to the tailrace of Lower Granite Dam for PIT-tagged wild subyearling fall chinook salmon in 1998 (top), 1999 (center), and 2000 (bottom), predicted from mean flows and water temperatures with (observed; from Table 1) and without (estimated; from Table 3) summer flow augmentation. The equation cohort survival = 140.82753 + 0.02648(flow) − 7.14437(temperature) was used to make both sets of predictions.

1955 (estimated from Figure 8 in Mains and Smith [1964]). Mean June temperatures for 1954 and 1955 were approximately 9°C and 11°C, respectively (estimated from Figure 8 in Mains and Smith [1964]). In contrast, the latest emigrating cohorts of fall chinook salmon during 1998–2000 were exposed to mean flows of 859–1,299 m^3/s and mean temperatures of 18.3–19.8°C.

The release of larger volumes of cooler reservoir water during the summer would provide present-day fall chinook salmon with velocity and temperature conditions more similar to their pre-dam counterparts that emigrated primarily in the late spring (Connor et al. 2002). Dworshak Reservoir and reservoirs upstream of Brownlee Dam, however, are the only two sources of additional water. The ability of fishery managers to obtain more cool water for summer flow augmentation from Dworshak Reservoir is limited by supply and competing demands. Dworshak Reservoir is routinely drafted to near-minimum operation levels, so releasing more water would reduce the probability of refill the next year. Release of larger volumes of water from Dworshak Reservoir earlier in the year to cover a larger percentage of the smolt migration would be difficult because of conflicts with summer recreation.

The release of the coldest water available from Dworshak Reservoir by use of the multilevel selector gates of Dworshak Dam would likely disrupt growth and seaward movement of fall chinook salmon that are still rearing in the lower Clearwater River when smolts from the Snake River are passing downstream in Lower Granite Reservoir (Connor et al. 2002). For example, the release of 6°C water in July 1994 decreased temperature in Lower Granite Reservoir from approximately 23°C to 17°C (Connor et al. 1998), thereby improving conditions for survival of smolts from the Snake River. However, the 6°C release also caused water temperature in the lower Clearwater River to decrease from approximately 19°C to 8°C (U.S. Geological Survey data collected at Spalding, Idaho) at a time when young fall chinook salmon were still rearing along the shoreline.

Increasing the supply of water available from reservoirs upstream of Brownlee Dam for summer flow augmentation would be difficult because of supply and competing demands. Cooler water cannot be released from Brownlee Reservoir because Brownlee Dam does not have multilevel selector gates. Consequently, the water released from Brownlee Reservoir for summer flow augmentation is relatively warm (e.g., 17.5–20.3°C; Connor et al. 1998). Development of the ability to selectively release cooler water from Brownlee Reservoir might be the most practical option for improving the effectiveness of summer flow augmentation, provided that cool, oxygenated water is available and impacts on native resident fishes would be acceptable to fishery managers. Cool water could be released from Brownlee Reservoir during summer, when fall chinook salmon smolts from the Snake River are passing downstream in Lower Granite Reservoir, without affecting water temperatures in the lower Clearwater River when fry and parr are still rearing.

Acknowledgments

D. Steele, C. Eaton, R. Nelle, R. Waitt, C. Larsen, J. Bretz, S. Bradbury, C. Piston, and many other employees of the U.S. Fish and Wildlife Service's Idaho Fishery Resource Office collected data. The staff at the Fish Passage Center of the Columbia River Basin Fish and Wildlife Authority provided flow data. C. Stein, D. Marvin, and the staff at the Pacific States Marine Fisheries Commission managed the PIT tag database. S. Smith provided statistical assistance. D. Bennett, P. Bigelow, J. Congleton, A. Graves, M. Scott, and K. Steinhorst reviewed drafts of the manuscript. The editor, an associate editor, David Fast, and one anonymous reviewer improved the manuscript. Funding was provided by the rate payers of the Bonneville Power Administration through contract number DE-AI79-91BP21708, administered by D. Docherty, M. Galloway, D. Praest, M. Beeman, and K. Tiffan.

References

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 *in* V. N. Petrov and F. Csaki, editors. Proceedings of the second international symposium on information theory. Akailseoniai-Kiudo, Budapest.

Anglea, S. M. 1997. Abundance, food habits, and salmonid fish consumption of smallmouth bass and distribution of crayfish in Lower Granite Reservoir, Idaho-Washington. Master's thesis. University of Idaho, Moscow.

Berggren, T. J., and M. J. Filardo. 1993. An analysis of variables influencing the migration of juvenile salmonids in the Columbia River basin. North American Journal of Fisheries Management 13:48–63.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society, Monograph 5, Bethesda, Maryland.

Connor, W. P., T. C. Bjornn, H. L. Burge, A. R. Marshall, H. L. Blankenship, R. K. Steinhorst, and K. F. Tiffan. 2001a. Early life history attributes and run composition and of wild subyearling chinook salmon recaptured after migrating downstream past Lower Granite Dam. Northwest Science 75:254–261.

Connor, W. P., and H. L. Burge. 2003. Growth of wild subyearling chinook salmon in the Snake River. North American Journal of Fisheries Management 23:595–600.

Connor, W. P., H. L. Burge, and D. H. Bennett. 1998. Detection of subyearling chinook salmon at a Snake

River dam: implications for summer flow augmentation. North American Journal of Fisheries Management 18:530–536.

Connor, W. P., H. L. Burge, R. Waitt, and T. C. Bjornn. 2002. Juvenile life history of wild fall chinook salmon in the Snake and Clearwater rivers. North American Journal of Fisheries Management 22: 703–712.

Connor, W. P., A. R. Marshall, T. C. Bjornn, and H. L. Burge. 2001b. Growth and long-range dispersal by wild subyearling spring and summer chinook salmon in the Snake River basin. Transactions of the American Fisheries Society 130:1070–1076.

Connor, W. P., R. K. Steinhorst, and H. L. Burge. 2003. Migrational behavior and seaward movement of wild subyearling fall chinook salmon in the Snake River. North American Journal of Fisheries Management 23:414–430.

Cormack, R. M. 1964. Estimates of survival from the sightings of marked animals. Biometrika 51:429–438.

Curet, T. S. 1994. Habitat use, food habits and the influence of predation on subyearling chinook salmon in Lower Granite and Little Goose reservoirs, Washington. Master's thesis. University of Idaho, Moscow.

Dielman, T. E. 1996. Applied regression analysis for business and economics. Wadsworth, Belmont, California.

Kjelson, M. A., and P. L. Brandes. 1989. The use of smolt survival estimates to quantify the effects of habitat changes on salmonid stocks in the Sacramento-San Joaquin rivers, California. Canadian Special Publication of Fisheries and Aquatic Sciences 105:100–115.

Kjelson, M. A., P. F. Raquel, and F. W. Fisher. 1982. Life history of fall-run chinook salmon, *Oncorhynchus tshawytscha,* in the Sacramento-San Joaquin estuary, California. Pages 393–411 *in* V. S. Kennedy, editor. Estuarine comparisons. Academic Press, New York.

Mains, E. M., and J. M. Smith. 1964. The distribution, size, time, and current preferences of seaward migrant chinook salmon in the Columbia and Snake rivers. Washington Department of Fisheries, Fisheries Research Papers 2(3):5–43.

Marine, K. R. 1997. Effects of elevated water temperature on some aspects of the physiological and ecological performance of juvenile chinook salmon (*Oncorhynchus tshawytscha*): implications for management of California's Central Valley salmon stocks. Master's thesis. University of California, Davis.

Matthews, G. M., G. A. Swann, and J. Ross Smith. 1977. Improved bypass and collection system for protection of juvenile salmon and steelhead trout at Lower Granite Dam. U.S. National Marine Fisheries Service Marine Fisheries Review 39(7):10–14.

NMFS (National Marine Fisheries Service). 1992. Threatened status for Snake River spring/summer chinook salmon, threatened status for Snake River fall chinook salmon. Federal Register 57:78(22 April 1992):14653–14663.

NMFS (National Marine Fisheries Service). 1995. Proposed recovery plan for Snake River salmon. NMFS, Portland, Oregon.

Ott, R. L. 1993. An introduction to statistical methods and data analysis, 4th edition. Wadsworth, Belmont, California.

Prentice, E. F., T. A. Flagg, and C. S. McCutcheon. 1990a. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. Pages 317–322 *in* N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester, Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

Prentice, E. F., T. A. Flagg, C. S. McCutcheon, and D. F. Brastow. 1990b. PIT-tag monitoring systems for hydroelectric dams and fish hatcheries. Pages 323–334 *in* N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester, Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

Raymond, H. L. 1979. Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966 to 1975. Transactions of the American Fisheries Society 98: 513–514.

Raymond, H. L. 1988. Effects of hydroelectric development and fisheries enhancement on spring and summer chinook salmon and steelhead in the Columbia River basin. North American Journal of Fisheries Management 8:1–24.

Skalski, J. R., S. G. Smith, R. N. Iwamoto, J. G. Williams, and A. Hoffman. 1998. Use of passive integrated transponder tags to estimate survival of migrant juvenile salmonids in the Snake and Columbia rivers. Canadian Journal of Fisheries and Aquatic Sciences 55:1484–1493.

Vigg, S., and C. C. Burley. 1991. Temperature-dependent maximum daily consumption of juvenile salmonids by northern squawfish (*Ptychocheilus oregonensis*) from the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 48:2491–2498.

Yearsley, J., D. Karna, S. Peene, and B. Watson. 2001. Application of a 1-D heat budget model to the Columbia River system. U.S. Environmental Protection Agency, Region 10, Final Report 901-R-01-001, Seattle.

Yoshiyama, R. M., F. W. Fisher, and P. B. Moyle. 1988. Historical abundance and decline of chinook salmon in the Central Valley region of California. North American Journal of Fisheries Management 18: 487–521.

Appendix: Flows and Temperatures in Lower Granite Reservoir

TABLE A.1.—Mean daily flows (m^3/s) in Lower Granite Reservoir with (observed) and without (approximated) summer flow augmentation, 1998 to 2000.

Date	1998		1999		2000	
	With	Without	With	Without	With	Without
Jul						
1	2,195	2,138	2,336	2,243	1,020	892
2	2,212	2,127	2,212	2,050	952	790
3	2,251	2,130	1,931	1,863	1,014	835
4	2,419	2,283	1,832	1,702	977	816
5	2,274	2,116	1,699	1,594	1,020	677
6	2,065	1,957	1,685	1,546	1,090	773
7	1,960	1,844	1,563	1,427	1,121	793
8	1,827	1,592	1,546	1,385	1,059	552
9	1,801	1,515	1,648	1,458	1,246	753
10	1,778	1,436	1,563	1,357	1,198	583
11	1,866	1,385	1,509	1,269	1,204	612
12	1,892	1,504	1,532	1,294	1,274	572
13	1,745	1,087	1,447	1,136	1,280	600
14	1,812	1,198	1,529	1,184	1,229	513
15	1,759	1,164	1,507	1,172	1,184	561
16	1,651	1,073	1,507	1,212	1,161	501
17	1,583	971	1,475	1,136	1,187	507
18	1,555	830	1,541	1,238	1,087	524
19	1,549	844	1,501	991	1,073	470
20	1,577	881	1,546	988	1,099	504
21	1,521	739	1,456	954	1,096	490
22	1,535	719	1,453	912	1,028	450
23	1,549	714	1,456	895	1,028	541
24	1,512	688	1,376	847	1,005	382
25	1,481	685	1,354	824	1,051	399
26	1,444	646	1,345	787	1,076	467
27	1,521	657	1,314	762	1,042	416
28	1,529	762	1,308	824	1,031	515
29	1,410	615	1,257	685	860	436
30	1,453	666	1,263	671	643	530
31	1,439	649	1,368	634	855	453
Aug						
1	1,450	830	1,357	617	833	408
2	954	765	1,382	632	864	428
3	963	612	1,323	615	784	402
4	1,283	705	1,303	702	748	337
5	1,167	586	1,266	660	833	413
6	1,201	634	1,175	615	776	360
7	1,065	592	1,181	640	759	351
8	1,107	671	1,198	753	745	354
9	943	436	1,116	555	733	326
10	1,065	510	1,141	671	813	362
11	1,045	484	1,054	600	813	377
12	1,104	524	1,028	547	733	280
13	1,136	552	1,164	694	787	368
14	1,087	496	1,028	697	773	362
15	1,028	496	1,090	702	750	297
16	960	524	1,073	657	753	261
17	827	396	1,170	711	799	365
18	954	445	1,022	595	767	252
19	974	413	1,025	578	858	408
20	1,065	566	1,070	544	787	354
21	932	521	1,051	637	787	391
22	787	487	906	538	649	329
23	716	498	898	462	677	365
24	719	490	997	569	691	354
25	688	487	892	487	671	331
26	683	552	960	569	685	428
27	575	462	901	467	583	360
28	617	402	912	583	677	354
29	697	544	827	527	566	362
30	592	541	810	552	513	346
31	507	334	782	476	518	368

TABLE A.2.—Mean water temperatures (°C) in Lower Granite Reservoir with (observed) and without (simulated) summer flow augmentation, 1998 to 2000.

	1998		1999		2000	
Date	With	Without	With	Without	With	Without
Jul						
1	16.6	19.0	15.8	16.2	18.8	17.8
2	17.5	19.8	15.9	16.6	19.1	18.2
3	18.1	20.1	16.0	16.9	19.4	18.7
4	18.7	20.1	15.8	16.8	19.4	18.9
5	19.0	20.3	15.8	17.0	19.0	19.2
6	19.0	20.1	15.7	17.0	18.7	19.3
7	19.3	19.7	15.7	16.8	18.4	20.0
8	19.7	19.7	16.0	17.0	18.0	20.1
9	20.1	19.5	16.8	16.7	17.9	20.3
10	20.6	19.7	17.3	17.1	18.1	19.7
11	20.7	19.5	17.7	17.3	18.3	19.2
12	20.8	20.0	18.2	18.1	18.0	19.3
13	20.5	20.4	18.6	18.5	18.0	19.3
14	20.2	20.6	18.9	18.7	18.2	19.1
15	20.0	20.7	19.3	19.0	18.6	19.0
16	19.7	20.7	19.7	19.3	18.9	18.8
17	19.9	20.7	19.6	19.8	19.1	19.3
18	19.9	20.8	19.8	20.1	19.0	19.6
19	20.4	20.9	19.6	20.3	19.0	19.7
20	20.4	21.3	19.2	20.2	18.9	19.9
21	20.9	21.8	19.1	19.9	19.1	20.3
22	20.7	22.0	19.1	19.9	19.2	20.3
23	20.1	22.2	18.9	19.7	19.4	20.2
24	19.7	22.4	18.7	19.8	19.6	20.6
25	19.5	22.6	18.9	19.5	19.7	20.8
26	19.7	22.7	19.1	19.3	19.5	21.0
27	19.7	23.0	19.2	19.4	19.4	21.2
28	19.7	22.9	18.9	19.9	19.5	21.2
29	20.2	23.1	19.0	21.0	19.5	21.6
30	20.1	23.3	19.3	21.2	19.4	21.7
31	20.2	23.7	19.8	20.8	19.4	21.8
Aug						
1	20.0	23.8	20.1	21.0	19.3	22.0
2	19.9	23.9	20.0	21.2	19.2	21.9
3	20.0	24.0	19.5	21.2	19.2	22.0
4	20.2	24.3	18.1	21.3	18.9	22.3
5	21.0	24.4	18.9	21.2	19.0	22.6
6	20.9	24.1	18.8	21.8	19.1	22.4
7	20.7	23.9	18.6	22.4	19.0	22.6
8	21.0	23.5	18.5	22.6	19.0	22.8
9	21.2	23.5	18.5	22.6	19.0	22.5
10	20.8	23.4	18.2	23.2	19.0	22.5
11	20.1	23.2	18.1	22.8	18.8	22.6
12	19.9	23.3	18.1	22.9	19.0	22.4
13	20.0	23.3	18.0	22.8	18.9	22.6
14	20.2	23.4	18.1	22.8	18.8	23.0
15	20.0	23.6	18.0	22.7	18.6	23.1
16	19.9	23.4	17.8	22.3	18.4	23.2
17	20.0	23.1	17.9	22.2	18.3	23.4
18	19.9	22.6	17.8	22.1	17.8	23.3
19	19.8	22.3	18.1	21.9	17.7	23.2
20	19.3	22.2	18.1	21.9	17.6	23.0
21	18.9	22.4	18.4	21.9	17.7	23.0
22	18.7	22.4	18.6	22.1	17.8	23.0
23	18.5	22.5	19.2	21.5	17.7	22.6
24	18.6	22.3	19.4	21.1	17.5	22.9
25	18.6	22.0	19.3	20.9	17.4	22.7
26	18.8	22.2	19.3	20.9	17.1	22.5
27	18.9	21.8	19.3	20.6	17.0	22.2
28	19.5	21.9	19.5	20.6	17.4	22.0
29	19.9	21.5	19.4	21.4	17.7	22.0
30	20.0	21.7	19.0	21.9	17.7	21.7
31	20.4	21.5	19.2	21.9	17.6	21.5